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Skleroptera, a new order of holometabolous insects (Insecta) from the Carboniferous

Skleroptera, новый отряд насекомых с полным превращением (Insecta) из карбона

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A new order of holometabolan insects is proposed for *Stephanastus polinae* Kirejtshuk et Nel, 2013 from the Upper Carboniferous of Allier, France (Gzhelian, Commentry) (Nel et al., 2013). It is considered a member of the superorder Coleopterida. It shares with the order Coleoptera sclerotised forewings, which demonstrate a simple and somewhat reduced Sc, a simple and concave RP, a convex RA, the M less convex than R and CuA, M also simple and basally fused with CuA (putative synapomorphy), but distally separating from it; stem of M+Cu well separated from R, the coxae do not project and the trochanters are short. The new order Skleroptera **ordo nov.** differs from the orders Coleoptera and Strepsiptera in the structure of the thoracic sclerites and venation of the forewings, particularly in the following character combination: the absence of lateral carina on the prothorax, the narrow separation of the bases of its forewings, the very narrow anal region of the forewings that widen apically and the absence of a sub-marginal anal (adsutural) vein going along the entire posterior margin of the tegmina. These unique characters of *Stephanastus* Kirejtshuk et Nel, 2013 suggest that this individual was somewhat laterally compressed (like some orthopteroids). This represents also an essential difference from body ground plan of the Coleoptera in general. It is hypothesised that the position of the new order within the superorder Coleopterida at the subclade level is as follows: Skleroptera + (Coleoptera [probably including Umenocoleidae sensu stricto] + Strepsiptera).

Новый отряд насекомых с полным превращением предложен для *Stephanastus polinae* Kirejtshuk et Nel, 2013 из верхнего карбона Алье, Франция (Гжельский ярус, Комментри), (Nel et al., 2013). Он рассматривается в составе надотряда Coleopterida. Вместе с отрядом Coleoptera он имеет склеротизованные передние крылья, которые показывают простую и отчасти редуцированную Sc, простую и вогнутую RP, выпуклую RA, M менее выпуклую, чем R и CuA, M также простую и основанием соедененную с CuA (предполагаемая синапоморфия), но отходящую от нее дистально, ствол M+Cu хорошо обособленный от R, тазики не выступающие, а вертлуги короткие. Новый отряд Skleroptera **ordo nov.** отличается от отрядов Coleoptera и Strepsiptera структурой грудных склеритов и жилкованием передних крыльев, в частности в следующей комбинации признаков: отсутствием бокового киля переднегруди, узкорасставленными основаниями передних крыльев, очень маленькими анальными областями передних крыльев, которые расширены кзади, и отсутствием пришовной анальной жилки, проходящей вдоль всего заднего края крыла. Эти уникальные признаки *Stephanastus* Kirejtshuk et Nel, 2013 позволяют предполагать, что эта особь была латерально сжата (подобно некоторым ортоптероидам). Эта особенность также представляет отличие от плана строения жуков в целом.

Выдвинута гипотеза о положении нового отряда внутри надотряда Coleopterida на уровне субклад: Skleroptera + (Coleoptera [возможно, включая Umenocoleidae sensu stricto] + Strepsiptera).

Key words: Insecta, Holometabola, Coleopterida, new order, Paleozoic, Carboniferous

Ключевые слова: Insecta, Holometabola, Coleopterida, новый отряд, палеозой, карбон

INTRODUCTION

Recently some Carboniferous holometabolans were described (Nel et al., 2013). Among these, *Stephanastus polinae* Kirejtshuk et Nel, 2013, from the Gzhelian (Commentry, Allier, France), was found to possess enough distinct characters to create a new order. In Nel et al. (2013), a new family Stephanastidae was proposed for this fossil however the present paper proposes a new order, and provides a broader comparison with related groups of pterygotes.

Depositories: AM – Australian Museum, Sydney; MNHN – Muséum National d'Histoire Naturelle, Paris; MCG – Museum of Comparative Zoology, Harvard University, Cambridge, USA; PrF UK – Přírodovědecká fakulta, Univerzita Karlova v Praze; WDC-CCFB – Wyoming Dinosaur Center-Crato, Wyoming.

RESULTS

Order **SKLEROPTERA** Kirejtshuk et Nel, ordo nov.
(Figs 1–5, 8)

Monotypic order; composition: family Stephanocoleidae Kirejtshuk et Nel, 2013 (type genus *Stephanastus* Kirejtshuk et Nel, 2013, type species *S. polinae* Kirejtshuk et Nel, 2013).

Diagnosis. Laterally compressed body; abdomen without cerci; forewing Sc simple and partly reduced; RP and M simple; concave M and convex CuA with a common stem separated from R (synapomorphies of superorder Coleopterida); very long CuP reaching distal eighth of forewing (possible plesiomorphy); anal veins very short at base of forewing (autapomorphies); forewings sclerotised and longer than abdomen, with very fine and dense iso-diametral cells forming regular rows generating intercalary veins along anterior edge, more diffuse near posterior margin; no adsutural line (submarginal anal vein along entire posterior edge), medial edge of forewings not forming straight adjoining margins, apices not meeting apically; very large area between C and R; coxae not projecting, trochanters apparently short; lateral prothoracic carina absent (no prohypomera).

Remarks. The diagnosis and description of *S. polinae* are given in the Supplementary information (on-line) of Nel et al. (2013). This diagnosis was also treated as the family diagnosis for Stephanastidae and with the above modifications; it is now used to characterise the new order.

The studied remains of *S. polinae* have the two superposed forewings forming subparallel veins of both wings exposed in the holotype print. These veins are equally exposed on the entire plane of wings because the structures of lower forewing seem to be shown through the comparatively soft (not heavily) sclerotised abdomen and probably posterior part of the thorax.

Etymology. The order name is formed from the Greek "skleros" (hard) and "pteron" (wing).

Comparison. The genus *Stephanastus*, differs from beetles (Coleoptera) in its laterally compressed body. It shows most similarities with the members of this order but maintains traces of the primary venation in the forewings (as in groups of Archostemata and particularly most Palaeozoic groups of this suborder). *Umenocoleus* Chen et T'an, 1973 (an enigmatic Mesozoic taxon de-

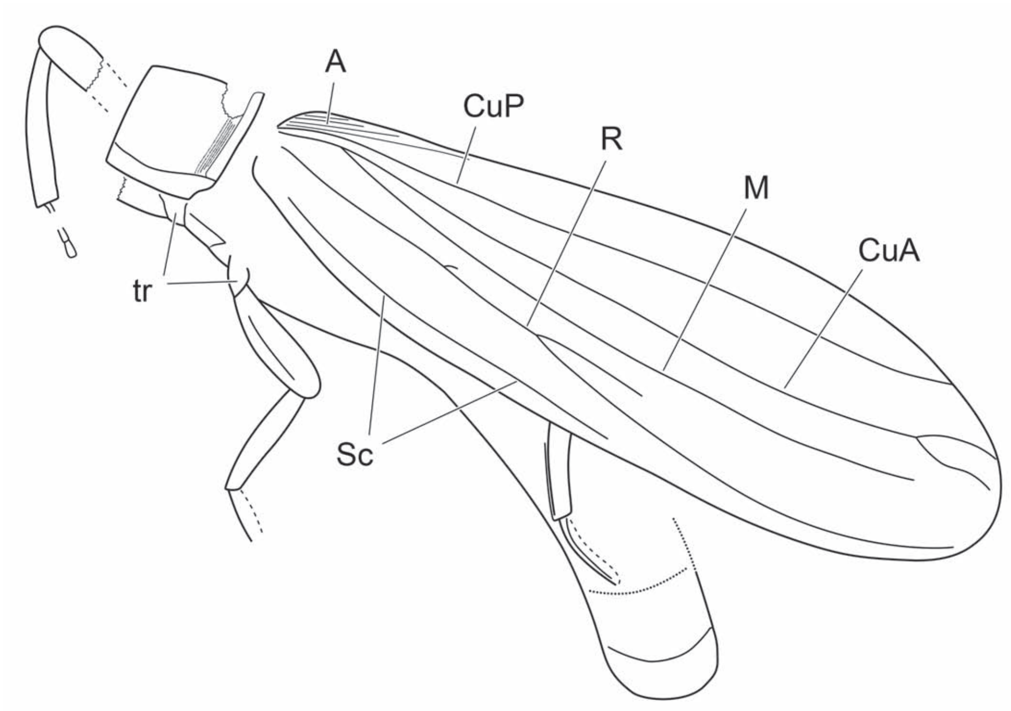


Fig. 1. Reconstruction of *Stephanastus polinae* (Skleroptera **ordo nov.**: Stephanastidae), holotype (MNHN.A.49011; Upper Carboniferious, Gzhelian, Commentry, Allier, France) (after Nel et al., 2013, with corrections). Body length (with elytra and without head); length 28.0 mm. Abbreviations: A, anal veins; CuA, cubitus anterior; CuP, cubitus posterior; M, median vein; Sc, subcostal vein; tr: trochanters.

scribed as Coleoptera, was later moved into the Protelytroptera, then associated with various elytriform cockroaches in the Blattaria, but recently considered as probably belonging to the stem-Coleopterida (Kirejtshuk et al., 2013). *Stephanastus*, together with the Coleoptera and *Umenocoleus* share sclerotised forewings (along with some Palaeozoic and Mesozoic true Protelytroptera, Dictyoptera, Glosselytrodea, "Hypoperlida" Perielytridae Zalesskii, 1948 (Rasnitsyn, 1980), and Hemiptera) with a network of small cells very similar to those of some beetles (especially visible in some Palaeozoic Tshekardocoleidae Rohdendorf, 1944, see Kirejtshuk et al., 2013). Nevertheless the most important characters shared by *Stephanastus*, Coleoptera and *Umenocoleus*, to the exclusion of all other holometabolous orders, include: Sc simple and somewhat reduced; simple concave RP and convex RA; M less convex than R and CuA, M also simple, and basally fused with CuA (putative synapomorphy), but distally separating from it; stem of M+Cu well separated from R. All these peculiarities are diagnostic for the order Coleoptera, although a simple RP occurs also in some representatives of the order Hymenoptera and a tendency for a reduction of Sc was expressed in the archostematan families that appeared in the Upper Permian, but not in the Lower Permian Tshekardocoleidae. Also, *Stephanastus*, like beetles in general, seems to have the non projecting coxae and short trochanters. Nevertheless, the very narrow anal region of the forewings of *Stephanastus*, the absence of lateral carina on its prothorax, probable narrow separation at the meetings of its forewings that widen apically suggest

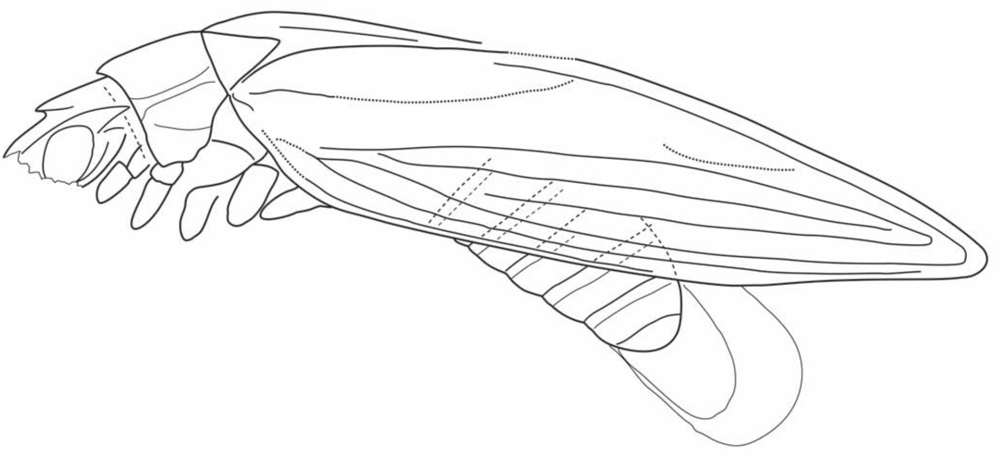


Fig. 6. Reconstruction of "*Moravocoleus*" *perditus* Kukalová, 1969 (Coleoptera: Archostemata: ?Tshekardocoleidae), holotype (PrF UK: 14/1968; Early Permian, Sakmarian/Artinskian, Obora, Boskovice Basin, Czech Republic). Body length 5.1 mm. Only the anterior veins of the forewing can be reconstructed; the conjunction of RP and A and also conjunction of branches of probable median veins at the forewing apex manifest some more similarity with Tshekardocoleidae than other archostematan families – see also Kirejtshuk et al. (2013).

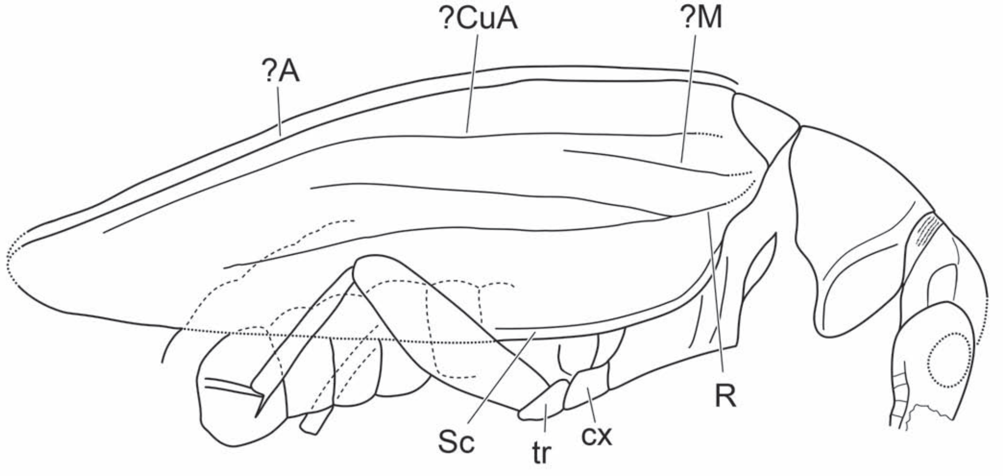
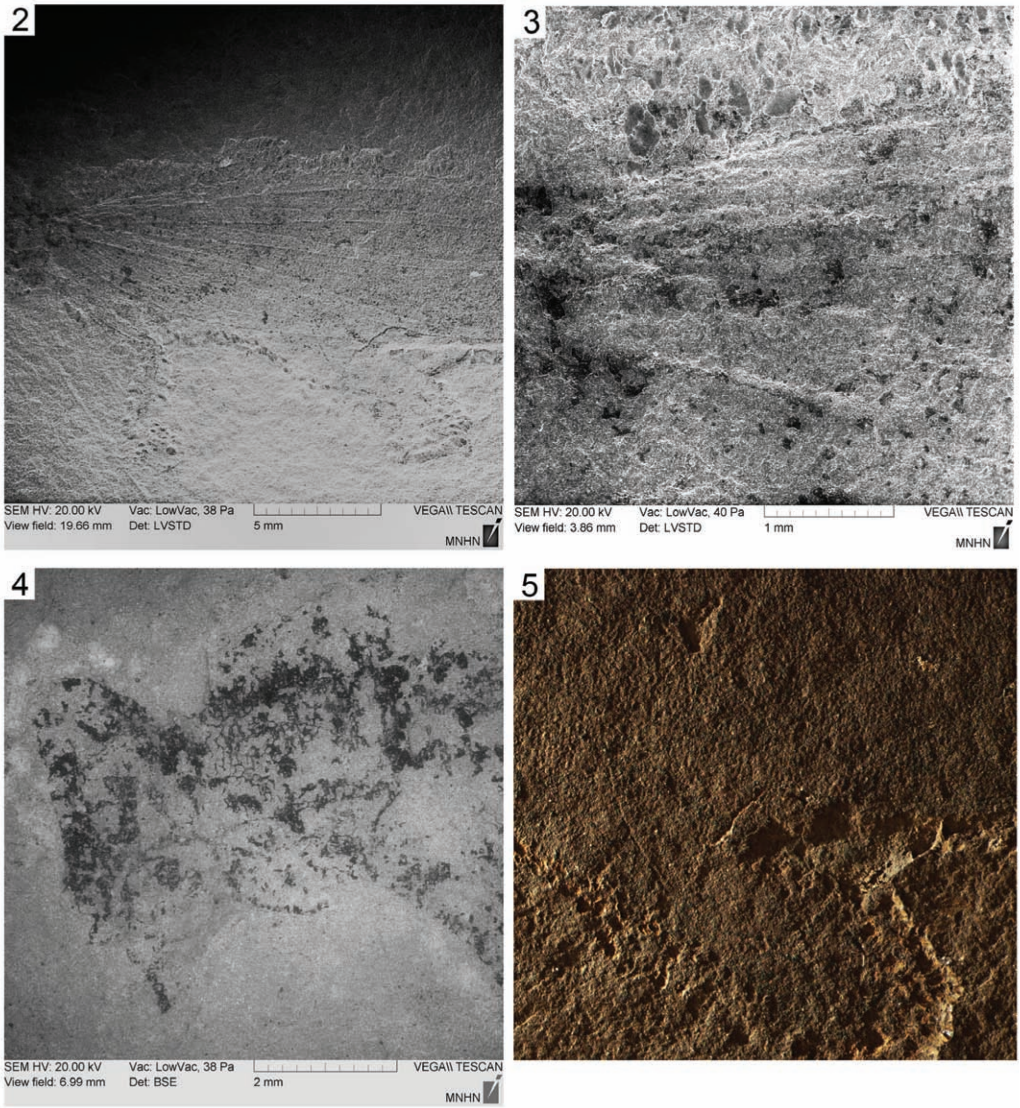


Fig. 7. Reconstruction of *Oborocoleus rohdendorfi* Kukalová, 1969 (Coleoptera: ?Asiocoleidae Rohdendorf, 1944), holotype (PrF UK: 7/1968; Early Permian, Sakmarian/Artinskian, Obora, Boskovice Basin, Czech Republic). Body length 11.2 mm. Abbreviations: ?A, possible anal vein; ?CuA, probable cubitus anterior; cx, metacoxa; ?M, probable median vein; R, radial vein; Sc, subcostal vein; tr, metatrochanter. The pattern of forewing venation is mostly correspondent with that in many Palaeozoic representatives of Asiocoleidae, particularly with members of the genus *Tetracoleus* Ponomarenko, 2009 (Aristov et al., 2013), although R of *O. rohdendorfi* is forked at the base. See also Kirejtshuk et al. (2013).



Figs 2–5. *Stephanastus polinae* (Skleroptera **ordo nov.**: Stephanastidae), holotype (MNHN.A.49011; Upper Carboniferious, Gzhelian, Commentry, Allier, France). Scanning electron microspcope (SEM) micrograms forewing and abdomen (**3**); forewing base (**4**); prothorax and legs (**5**); photograph of abdomen (Olympus SZX-9 stereomicroscope) (**6**). Body length (with elytra and without head) 28.0 mm.

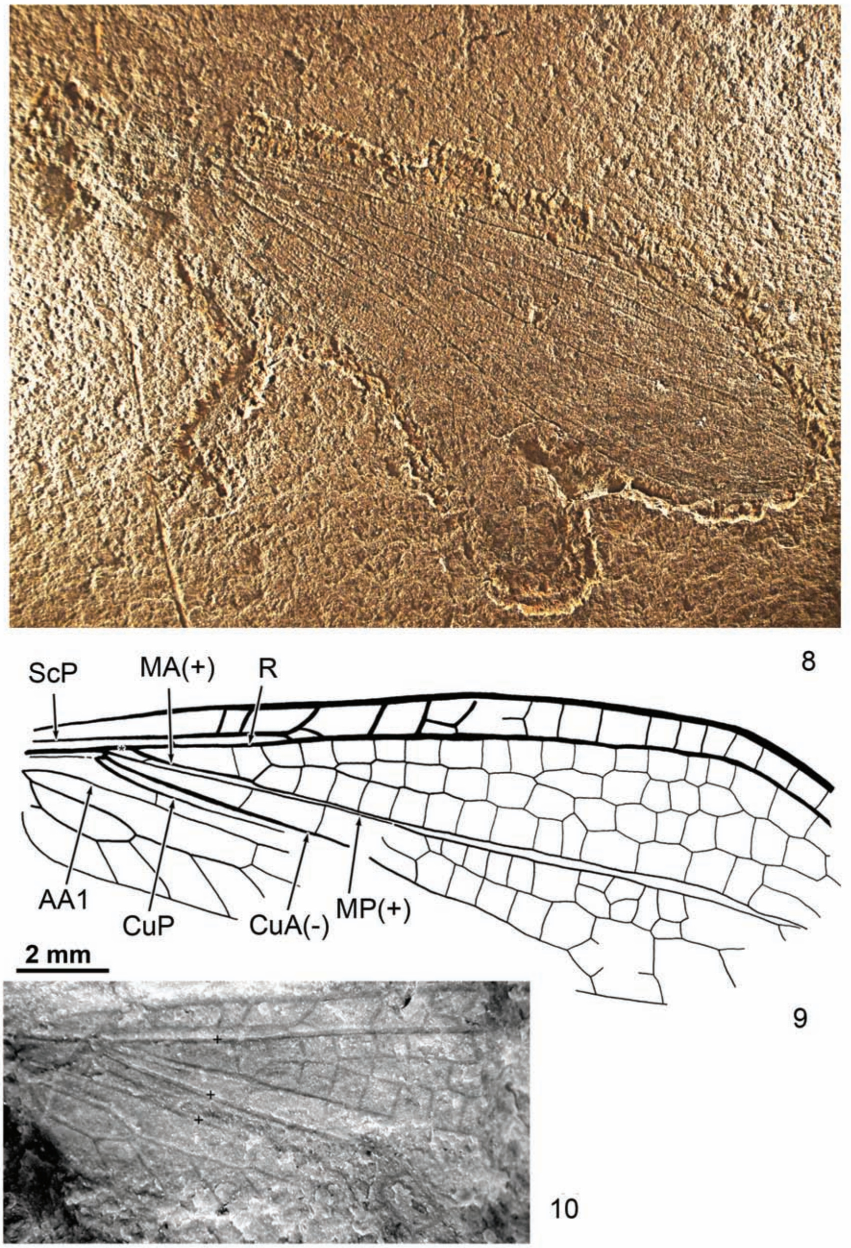


Fig. 8–10. *Stephanastus polinae* (Skleroptera **ordo nov.**: Stephanastidae), holotype (MNHN.A.49011; Upper Carboniferious, Gzhelian, Commentry, Allier, France) (abdomen, Olympus SZX-9 stereomicroscope) (**8**); *Eoglosselytrum perplexa* (Riek, 1953) (Glosselytrodea: Jurinidae Zalessky, 1929), specimen AMF128457/AMF128461 (Upper Permian, Wuchiapingian/Changhingian, New Castle, Sydney Basin, Australia): drawing of hindwing (**9**) and photograph of hindwing base (**10**) (after Béthoux et al., 2007, with corrections). Designations of veins in *S. polinae* see Nel et al. (2013). Body length of the latter (with elytra and without head) 28.0 mm. Scale for drawing (9) and photograph (10) of *Eoglosselytrum perplexa*. Abbreviations: AA1, first anal anterior; CuA, cubitus anterior; CuP, cubitus posterior; MA, median anterior; MP, median posterior; R, radial vein; ScP, subcostal posterior; (+), convex vein; (-), concave vein.

that this genus is characterised by a natural partial lateral compression of its body (like some orthopteroids), which represents an essential difference from the body ground plan of the Coleoptera in general. Finally, the forewing venation of *Stephanastus* differs from that of Coleoptera in the absence of a sub-marginal anal (adsutural) vein along the posterior margin of the tegmina, which could be regarded as a plesiotypic feature of the Coleopterida.

Some fossils are somewhat similar to *Stephanastus* and Coleoptera but with characters not clearly expressed. Two of them described by Kukalová (1969) as Protelytroptera and transferred by Ponomarenko (1969) to Coleoptera are needed to be mentioned because they were fossilized in the lateral position and demonstrate appearance and body-size with overlapping veins of two forewings which could be compared with *Stephanastus* (see Figs 7–8 and captions under them).

Stephanastus has a superficial similarity to some representatives of Glosselytrodea (showing conformity in the fore- and hindwing venation, reduction of anal region and sometimes soft distal part of body) with M and CuA of their sometimes tegminous forewings fused sub-basally and with a body rather high but not dorsoventrally compressed. However, the latter group are distinct from *Stephanastus* in having the RP(+MA?) with more than three branches; the two veins running parallel from wing base to wing apex in the mid section of the wing being anteriorly the convex MA and posteriorly the concave MP, after the reinterpretation of the wing venation proposed by Béthoux et al. (2007) (see also Martynova, 1961: pl. 20, figs 130–132), (in contrast to the concave MP and the convex CuA in *Stephanastus*), and not the vein MP and an anterior branch of CuA [as proposed in Béthoux et al (2001) and in Rasnitsyn and Aristov (Aristov et al., 2013)], because under this interpretation, these two veins should be respectively concave and convex, which is not the case (Figs 9–10); the shorter CuA and CuP (the latter scarcely extending beyond the midlength of the forewing), the forewings without clear sclerotisation and dense isodiametric cells forming intercalary pseudoveins; and the long coxae.

Stephanastus is strikingly different from members of the Hemiptera with sclerotised forewings (and in fact with all Paraneoptera) in the fused M+CuA which are completely separated from the radial stem at the wing base (Nel et al., 2012). Some Dictyoptera also have more or less sclerotised forewings. Especially the Blattodea that belong to the so-called “Umenocoleoidea” sensu Vršanský (2003) or Bechly (2007) (see Kirejtshuk et al., 2013), share with the Coleoptera (but not *Stephanastus*) the presence of a sub-marginal anal vein along the entire posterior edge of the forewing (Fig. 12). Nevertheless, these cockroaches have a RA with anterior branches, unlike the Coleoptera and *Stephanastus*. *Stephanastus* differs from the Perielytridae (*Perielytron* Zalleskii, 1948) in the simple RP, M, CuA in the forewing (Rasnitsyn, 1980).

The Protelytroptera is an enigmatic group of Permian insects with sclerotised tegmina, currently thought to be related to the Dermaptera. They strongly differ from *Stephanastus* in the presence of cerci. These insects also have a sub-marginal anal vein along the entire posterior edge of the forewing. Nevertheless their forewing venations are very different (after Carpenter, 1992): *Protelytron*-type (Fig. 11): median vein well separated from the cubital veins CuA and CuP (which have relatively long common stem), RA simple; *Phyllelytron*-type: median vein and CuA fused and separated from CuP (also present in *Planelytron* Kukalová, 1965, etc.). The Protelytroptera is possibly a polyphyletic group.

DISCUSSION

The sclerotisation of forewings happened many times in the history of the pterygotes and such processes were often accompanied by parallel transformations of

the vein pattern of the sclerotised wings, including some simplification of the forewing venation in general. These conditions sometimes resulted in confused systematic interpretations of the studied fossils with similar forewings (Ponomarenko, 1969; Kirejtshuk et al., 2013; Nel et al., in preparation; etc.). *Stephanastus* demonstrates both sclerotisation of the forewings and simplification of their venation. Nevertheless, the peculiar structural details of the venation give some diagnostic characters for each group with the sclerotised forewings (see above).

The newly proposed order which is related to the Coleoptera should be regarded as Holometabola (= Endopterygota). Taking into consideration the ecological concept of the origin of Coleoptera, a group that evolved in subcortical space and interstices of Palaeozoic wood (Crowson, 1960; Ponomarenko, 1969; Kirejtshuk, 1991; Kirejtshuk et al., 2013; etc.), the dorsoventral body compression of the Coleoptera should be recognised as a very probable initial (plesiotypic) feature of the order which was continued in all further phyletic lineages of the Coleoptera (even in groups not associated with wood). Therefore the lateral body compression of *Stephanastus* seems to be a secondary deviation from the basal stem of the Coleopterida. It can be supposed that *Stephanastus* had an adult life style connected with dwelling on the surface of substrates rather than inside them.

The main differences between *Stephanastus* and beetles + *Umenocoleus* are as follows and support a sister-group relationship with the (Coleoptera + Strepsiptera): prothorax forming a comparatively long monolithic sclerite covering the dorsum and most of the lateral surfaces, no lateral pronotal carina (no evident prohypomera, plesiomorphy compared to the situation in Coleoptera), CuA with two very short branches near apex instead of being simple (possible autapomorphy); CuP very long, rather than being shorter than CuA (plesiomorphy, character also present in Neuropterida); anal area and anal veins strongly reduced (autapomorphy), but not forming an "adsutural line" (submarginal anal vein) along entire posterior forewing edge (plesiomorphy). A further plesiomorphy shared with the Tshekardocoleidae is the very broad costal and subcostal areas, which is not as broad as in many of the more derived beetle lineages.

The legs of *Stephanastus* apparently have short trochanters and non-projecting coxae. These features are shared with Palaeozoic Coleopterida (probable symplesiomorphies); however, the femora and tibiae are markedly longer than those in Permian beetles. However if the absence of submarginal anal vein of forewing in Skleroptera seems to be a plesiomorphy, the reduction of the entire anal area of skleropteran forewings is certainly apotypic feature. One very important character distinguishing *Stephanastus* from Coleoptera is the structure of the prothorax. *Stephanastus* seems to maintain the initial structure of a prothorax with the pronotum having steeply sloping sides without the division into a dorsal section with sloping lateral sections (prohypomera, apomorphy of Coleoptera).

The order Strepsiptera has a rather unclear origin, although in most interpretations this order is linked with the Holometabola. Some researchers (Kathirithamby et al. 1984; Kathirithamby, 2000; Rasnitsyn 2002; etc.) consider that this order should be placed among the holometabolans without a precise position, but others argue their position should be with (or even inside) the Coleoptera (Handlirsch, 1903; Crowson, 1960; Kukalová-Peck & Lawrence, 1993; Niehuis et al., 2012; etc.) or even with the Diptera (Whiting & Wheeler, 1994; Whiting et al., 1997; etc.). The male body of the order Strepsiptera is not dorsoventrally compressed and lacks lateral prothoracic carina. The species of this order, in contrast to *Stephanastus*, possess more or less strongly projecting coxae, lack trochanters; the males possess strongly transformed forewings and strongly reduced pro- and mesothoraces.

Taking into consideration that the Skleroptera have some superficial similarity with members of different holometabolan orders (including plesiotypic absence of the prothoracic lateral carina separating the prohypomeron), the new order differs from these others in lacking projecting coxae and having a unique forewing venation (see above), although some general plesiotypy of this order in comparison with Coleoptera is possible. The separation of the Skleroptera from other Coleopterida could have happened when the dorsoventral compression of the body had not been rigidly set in the structural organization of beetle. If the Strepsiptera had phyletic links with Coleoptera, its mode of life is scarcely close to the basal pattern for the Coleopterida, although this link could be rather old (at least before the appearance of the cucujiformian beetles, including the Lymexylidae Fleming, 1821 and Rhipiphoridae Gemminger et Harold, 1870, with similarities in metamorphosis and lifestyle with Strepsiptera, although this link most probably much earlier than the Coleoptera diversified). Thus, *Stephanastus* may be considered as a representative of the stem-group to Coleopterida (= Coleoptera + Strepsiptera). It demonstrates for the first time a Pennsylvanian, progenitor of this hyperdiverse lineage that was already suspected after the recent discovery of Tshekardocoleidae in the Lowermost Permian of Germany (Kirejtshuk et al., 2013). Having summarized the current knowledge on Coleoptera and its close relatives, it is hypothesized that the superorder Coleopterida comprises the subclades: Skleroptera + (Coleoptera [probably including Umenocoleidae Chen et T'an, 1973, s. str.] + Strepsiptera).

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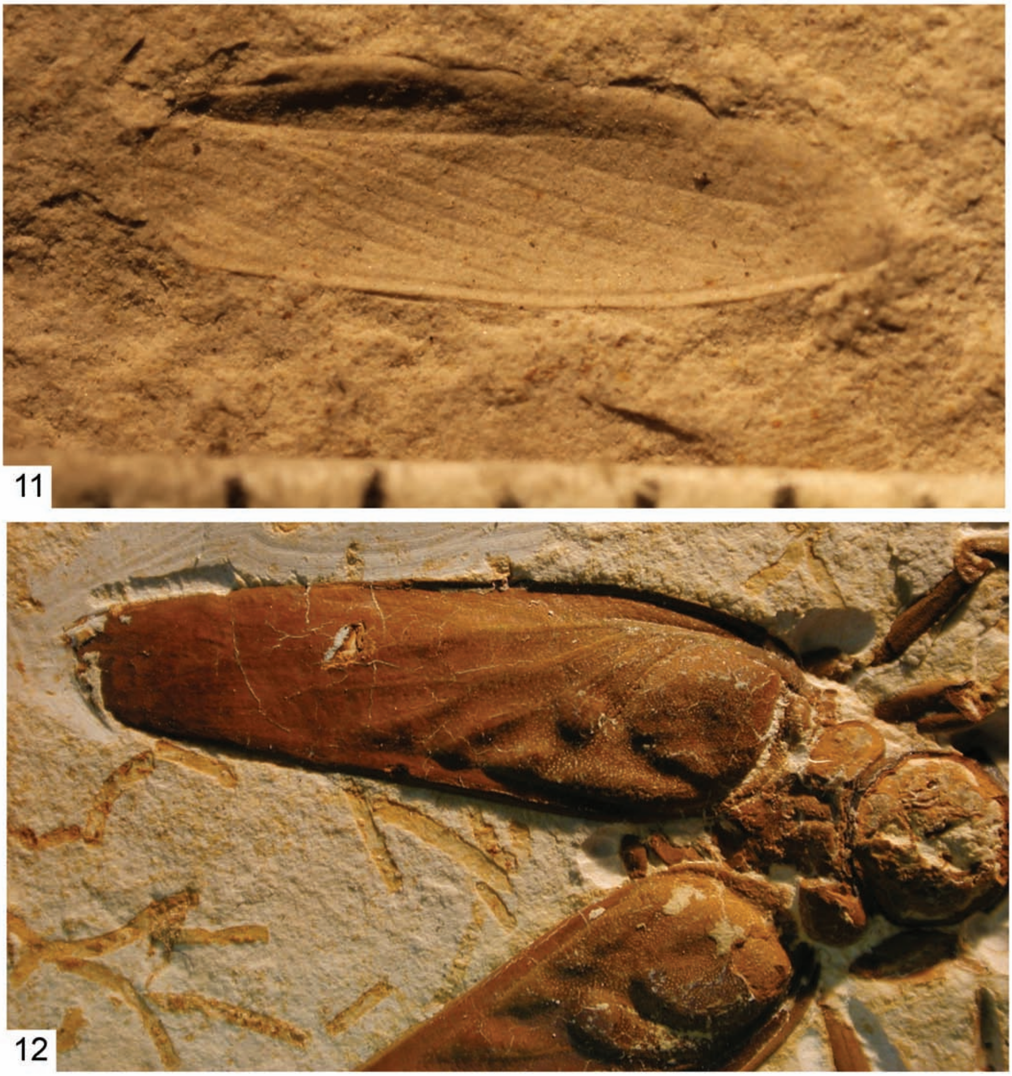
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Figs 11–12. Fossil Polyneoptera. *Protelytron angustum* Carpenter, 1933 (Protelytroptera: Protelytridae Tillyard, 1931), holotype MCZ N 3371 (Lower Permian, Artinskian, Elmo, Kansas, USA); length of tegmina 6.0 mm (**11**); Dictyoptera with sclerotised tegmina, undescribed cockroach of "umenocoleoid"-type (sensu Vršanský, 2003), WDC-CCFB (Lower Cretaceous, on or near the Aptian/Albian boundary, Crato, Araripe Basin, Brazil; length 23.0 mm (**12**).